甘藷光合產物與產量

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摘　要

甘藷的供源與積儲關係曾被廣泛地探討，以期對甘藷產量提供更多的資訊，從而克服生產上的限制因子。甘藷品系間供源能力與積儲强度存在著極大的差異。這兩者對甘藷產量都有極大的影響力。僅管如此，種種跡象仍顯示積儲能力比供源强度更能影響光合作用及養分輸送，而積儲强度更控制著乾物的累積及塊根產量的形成。另一方面，由於甘藷的供源因子比積儲因子複雜，因此利用遺傳方法及生產管理方法之改善來强化積儲强度應比提高供源能力更能有效提高產量。當積儲强度已予强化，而致供源能力形成產量的限制因子時，產量的突破則需針對供源與積儲作整體性的改善。

(關鍵詞：甘藷、供源、積儲、乾物產量、乾物分配、產量)

內　容

甘藷是熱帶地區的重要糧食作物，主要的食用部位爲貯藏根。其產量形成決定於數種形態及生理特徵。甘藷產量是：植株數／單位土地面積×儲藏根數／植株×儲藏根平均重。貯藏根數目和其平均重受到許多生理活動的影響。環境造成的單一生產因子的改變常會連帶導致植株其它生產因子的調整。隨著貯藏根的分化，決定塊根發育的潛力；然後細胞分裂及生長決定貯藏根的大小；最後，澱粉顆粒的合成決定澱粉在細胞的密度 (Hahn & Hozyo 1984)。貯藏根之生產潛力基本上決定於總乾物之產量，及轉化爲貯藏根的乾物之比例。葉子經由光合作用成爲乾物生產的供源，而貯藏根則是經濟栽培上主要的積儲器官。本文將循下列途徑討論供源－積儲的關係，藉以改良甘藷：(1)定義植株中的總乾物量，(2)調查乾物分配與產量形成的關係，(3)記錄乾物量及分配之種間差異。分析這些特徵和供源－積儲關係應有助於確認主要生產限制因子。

一、供源潛力

總乾物量之提高有賴於有效日射量、作物之光合成能力、及此能力之持續性。增加輻射或光合成活動及延長這些活動的時間應該也能增加乾物量。甘藷葉之淨光合成有品系間的差異。成熟葉之最大淨光合成率差異在12.0至38.1mg $CO_2/dm^2/h$ (Bhagsari 1981；Bhagsari and Harmon 1982；Fujise and Tsuno 1962；Tsuno and Fujise 1964b)之間。葉之光合成活動和二氧化碳擴散係數與總乾物量有直接關係(Bhagsari and Harmon1982；Hahn and Hozyo 1983)，而光合成二氧化碳差額也直接與作物在田間所測之生長率有關(Agata

and Takeda 1982b)。光合成活動之差異也受外界環境因子 (Bhagsari andHarmon 1982) 諸如高土壤濕度、高溫及黏重土壤 (AVRDC 1988；Martin *et al.* 1988)，以及植株內部因子(Kays 1985) 如葉之氮含量、葉綠素含量及氣孔密度 (Bhagsari 1981 , Tsuno and Fujise 1965a)等之調節。然而，乾物量及光合成活動的種間差異及其影響所及的生理過程和形態特徵時常與貯藏根產量無關(Bhagsari 1981；Bhagsari and Harmon 1982；Sadik 1972)。總乾物量及最後貯藏根產量間之缺乏直接關聯顯示與供源潛勢無關之生理及生化過程也影響最後產量。 Bhagsari & Brown (1988)認爲葉面積和光合成率的負相關可能是光合成率與產量無關的原因之一。甘藷生產新葉直到收成。它提供足夠的乾物量以便降低新葉與發展中貯藏根的競爭。Lemon *et al.* (1971)估計大約只有7%光合成可利用之可見光轉化爲乾物量。根據3至4個樹冠早期覆蓋面佳之品種所推算出的理想的葉面積指數 (Loomis and Williams 1963)，作物在150天生長期每天接受 450 cal/cm^{2}之能量，其淨乾物產量估計約 36 t/ha (表1)。

Table 1. Estimation of potential yield by a sweet potato crop surface receiving 450 cal/cm^2/day during 150-day growing period.

1	Visible radiation, 400-700 nm (45% total)	202	cal/cm^2
2	Less 20% albedo loss & inactive absorption	162	cal/cm^2
3	[CH_2O] produced (1 umole CO_2/1.16 cal)	140	umole/cm
4	Less 40% respiration loss	84	umole/cm^2
5	Daily net [CH_2O] production (30 g/mole)	25	g/m^2
6	Net [CH_2O] production in 150 days	3.75	kg/m^2
7	Net [CH_2O] of economic part (45% HI)	1.69	kg/m^2
8	DM of economic part (75% efficiency)	1.27	kg/m^2
9	Potential storage root yield (65% moisture)	36.3	t/ha

二、積儲強度

貯藏根的產量決定於貯藏根生長時可利用的乾物量、同化養分輸送率及量，及根蓄積同化物的能力。一般認爲積儲，即貯藏根之數量及大小，接受同化物的能力是影響貯藏根產量的一個主要因素。甘藷的貯藏根得自於地下莖之節所衍生的不定根，而其萌發則是初次形成層高度活動的結果 (Wilson 1982)。另一方面，貯藏根膨大－澱粉於此時期蓄積－是異形形成層細胞分裂的結果。軸的中心部份的薄壁細胞所產生的異形形成層時常以圓柱形出現，環繞木質元素群，其寬度可能一直增加直到相當大的範圍形成(Kokubun 1973)。一般認爲同化物輸送至貯藏根與異形形成層之發育，及同化養分自異形形成層擴散到中心柱的貯藏薄壁細胞有直接關聯 (Kato *et al.* 1972)。

植物生長調節劑可促進貯藏根的形態發育和生長(Wilson 1982)。Auxins 可增加貯藏根數(Jimenez and Garner 1983)，而cytokinins則與貯藏根的發展和膨大有關(Matsuo *et*

al. 1983; McDavid and Alamu 1980)。Auxins和cytokinins的總量隨貯藏根的發育而增加，而貯藏根則比鬚根含有較高量的auxins和cytok-inins (AVRDC 1990a)。Cytokinins可能有助於細胞分裂和初次及二次維管束形成層之擴張、以及隨後的貯藏根的大薄壁細胞的長大，而auxins可能有助於二次維管束的產生。

形成層活動也需要鉀 (AVRDC 1990a; Reshid and Waithaka 1988; Tsuno and Fujise 1965b)。鉀也可能影響澱粉合成的活動(Murata and Akazawa 1969)。確定關鍵時期正跟確定控制貯藏根新陳代謝活動所需植物生長調節劑的確切劑量一樣重要。

三、限制因子－供源潛力或積儲強度？

貯藏根產量不只由供源控制，也由積儲控制。生產是受供源還是積儲限制很難確定。因此必須考慮供源或積儲可能限制生產的證據。

(一)積儲的功效

為判斷限制甘藷生產的是供源或積儲，本實驗廣泛地使用一組繁殖系的所有可能嫁接組合 (AVRDC 1988 and 1990a; Hozyo 1977; Hozyo and Kato 1973 and 1976a and b; Hozyo and Park 1971; Kato and Hozyo 1974 and 1978; Li and Kao 1985b; Nakatani *et al.* 1988a and b)。貯藏根的生長率和光合成活動與貯藏根產量的關係分別根據貯藏根發展、光合成活動、及乾物分配的差異予以研究。一般說來，不論供源潛力如何，高積儲接木的產量比低儲積接木大(圖1)。低供源／高積儲或高供源／低積儲轉換接木之總乾物(圖2)及貯藏根產量(圖1)介於自體嫁接繁殖系之間。嫁接處理也顯示繁殖系發展貯藏根的早晚決定於由其積儲而非供源 (Hozyo *et al.* 1971)。因此，高積儲接木顯然比低積儲接木對供源有較大反應；同樣地，高供源接木顯然對積儲有較大功效(Hahn 1977)。

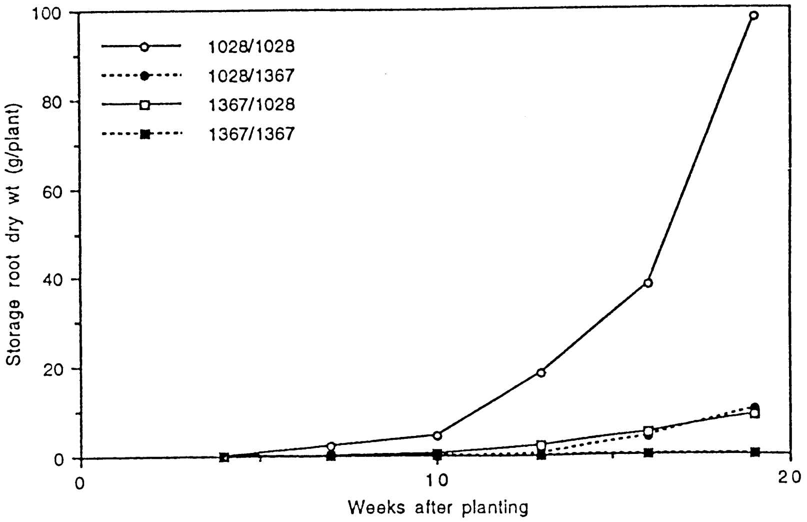

Figure 1. Storage root dry weight of self and reciprocally grafted(scion/stock) plants of wo sweet potato clones, CN 1028-15 and CN 1367-2, at different growth stages.

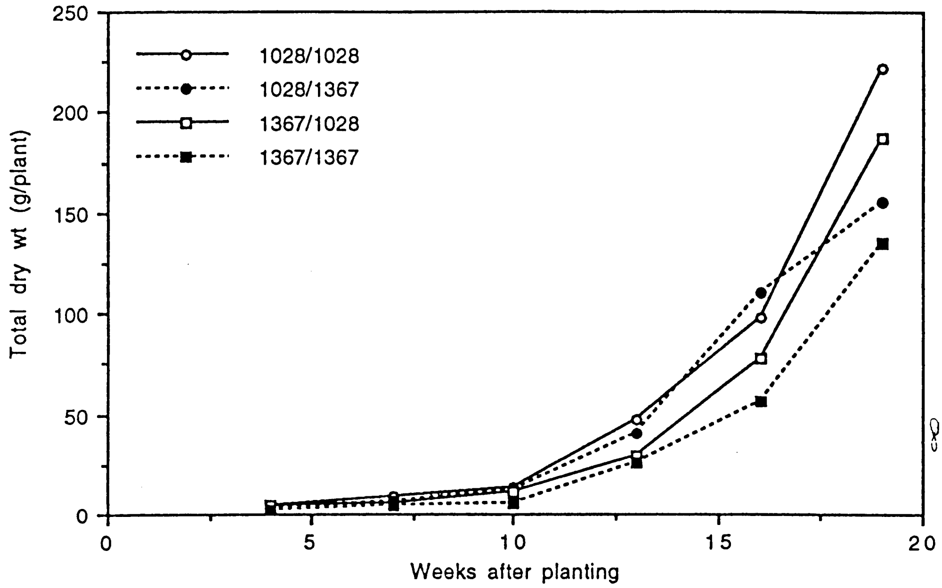

Figure 2. Total dry matter production of of self and reciprocally grafted(scion /stock) plants of two sweet potato clones, CN 1028-15 and CN 1367-2, at different growth stages.

化學分析顯示高供源的單葉嫁接在整個生長期間葉部均維持大量的可溶性糖，但只在早期生長階段有大量的澱粉 (AVRDC 1990a)。由於葉的光合成率和二氧化碳的擴散係數相關，高積儲或貯藏根的快速膨大引發最高淨光合成率(圖3)和二氧化碳擴散係數 (AVRDC 1988; Hozyo and Kato 1976; Kato and Hozyo 1978; Nakatani *et al.* 1988a)。一般認為積貯能力對樹冠的光合成也有很大的效應(Agata and Takeda 1982b)。高積儲接木也藉降低葉肉細胞抵抗力而非氣孔抵抗力來提高葉部的擴散係數(Nakatani 1988b)。由於澱粉是光合成過程的終極產物，葉部光合成的改變似乎與核糖二磷酸炭酸酵素活性有關，並且依靠積儲控制葉部澱粉含量。

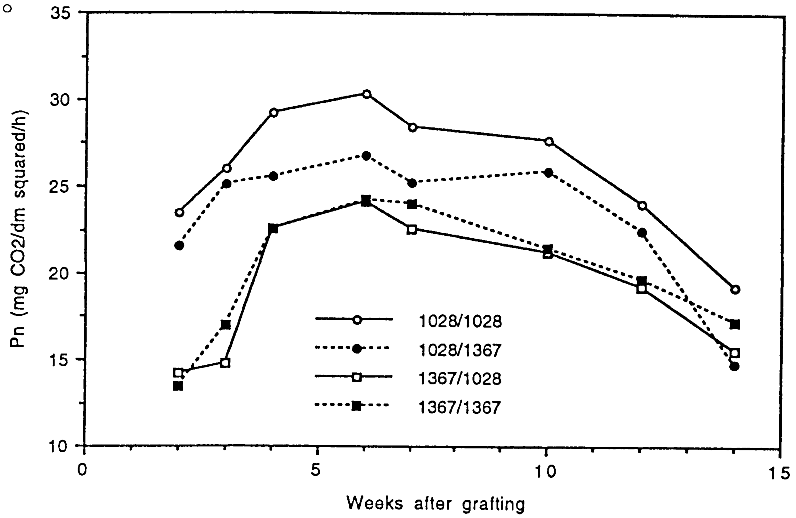

Figure 3. Changes in net photosynthetic rates of self and reciprocally grafted (scion/stock) leaf cuttings of two sweet potato clones, CN 1028-15 and CN 1367-2, during the growth period of 2 to 14 weeks of growth.

高積儲接木在發展中的貯藏根和鬚根累積大量的可溶性糖 (AVRDC 1990a)。但是鬚根中的可溶性糖在生長階段後期下降，也許因爲發展中的貯藏根對可溶性糖有較大的需求以進行澱粉之合成，而造成給鬚根的供應量較低。相反地，低積儲接木在發展中貯藏根吸收的可溶性糖較少，但在貯藏根以外的地方蓄積相當多的澱粉 (AVRDC 1990a)。在這些接木中，同化養分顯然不是輸入發展中貯藏根而是轉移到其他植株部位。而且，低積儲接木的葉在生長階段後期比高積儲者累積較多澱粉，暗示葉部合成之澱粉並未運離葉部。因此，這可能是葉部光合成活動在光合成過程受回饋抑制而降低的原因(Nakatani *et al.* 1988a; Tsuno and Fujise 1965a) 。這顯然降低了總乾物生產 (AVRDC 1990b; Bhagsari and Harmon 1982; Nakatani *et al.* 1988a) 。因此回饋抑制對光合成活動的影響可能是主導乾物生產的一個重要因子。環境或內部指令因此可能藉著限制輸送率對光合成產生不良影響(Gifford *et al.* 1984)。

高供源或低積儲接木增加葉比重，而高積儲接木則減少葉比重 (AVRDC 1990a)。葉比重的增加代表柵狀組織厚度的增加，並且可能表示葉部物質的不流動性。在這情況下，葉顯然從供源器官變成積儲器官。

低積儲葉的解剖觀察也顯示大量澱粉顆粒沈積在葉中肋基本組織和維管束組織的薄壁細胞。另一方面，高積儲接木的發展中貯藏根有較多的異形形成層數(表2)及大薄壁細胞(表3)，還有大量的澱粉顆粒累積在這些細胞的內部或周圍。這些觀察證實先前的主張：低積儲造成葉部澱粉的累積，並影響整個養分輸送的途徑，而貯藏根的膨大則靠異形形成層的分化。

Table 2. Number of anomalous cambium per cross section of storage root as changed with age.

Grafting combination (scion/stock)	Weeks after grafting			
	2	3	6	12
CN1028/CN1028	0	32[a1]	124[a]	128[a]
CN1028/CN1367	2	2[b]	51[c]	92[b]
CN1367/CN1028	0	34[a]	76[b]	96[b]
CN1367/CN1367	0	5[b]	25[d]	60[c]

1.Mean separation within columns by Duncan's multiple range test at P = 0.05.

Table 3. Average cell size (x 10 mm) of storage root parenchyma cells at 6 and 12 weeks after grafting.

Grafting combination (scion/stock)	Weeks after grafting	
	6	12
CN1028/CN1028	4.59±1.03	8.03±1.05
CN1028/CN1367	3.26±0.39	5.47±0.63
CN1367/CN1028	4.25±0.58	6.32±0.76
CN1367/CN1367	2.86±0.78	5.88±0.86

1. Each value is the mean of 23 determinations ±SD.

㈡分配

同化物從葉部移出的速率對貯藏根的發展似乎比對葉面積的增加更重要(Austin and Aung 1973)。因此，乾物分配對於貯藏根的最後產量有決定性的影響 (Bouwkamp 1983; Pardales and Belmonte 1989)。高產量品系通常能累積較多的同化物於貯藏根中(Bhagsari and Harmon 1982) 。營養生長不太多的繁殖系貯藏根產量最高，亦即，在膨大期葉生長的受限與高產量有關 (Bouwkamp 1983)一極可能是因爲同化物從葉到發展中的根的重新分配。因此，影響這種分配的主要因子可能是輸送效率。韌皮部輸送在同化物的裝載、運輸及卸下方面可能扮演重要角色(Kays 1985)。但是一般認爲輸送效率的先天差異起因於積儲發展期間限制養分輸送速度和速率而不是韌皮組織的數量 (De Calderon *et al.* 1983; Kato and Hozyo 1976, 1978; Kays *et al.* 1982, 1987)。

收穫指數表示貯藏根和植株其餘部份同化物的相對分佈。甘藷繁殖系間收穫指數的差異範圍在5至75％之間(AVRDC 1990b; Bhagsari and Harmon 1982; Bouwkamp 1983; Huett 1976; Li and Kao 1985a)。收穫指數亦受植物營養和其他栽培和環境因素的影響（Kays 1985）。高產量繁殖系通常比低產量者有較高的收穫指數(AVRDC 1990b; Huett 1976; Li and Kao 1985a; Lowe and Wilson 1974)；高收穫指數表示這些繁殖系之貯藏根具有高比例之相對生物產量。高積儲接木之收穫指數也比低積儲者高(AVRDC 1988)。相反地，高積儲低供源接木比低積儲高供源接木保持較高的收穫指數，稍高之產量但是較低的總乾物量。這可能是由於低供源導致採收期的低乾物總量。因此，即使收穫指數似乎比總乾物量重要，還是需要高供源與高積儲配合來才能表現其潛力。

㈢同化物的供應

研究結果顯示限制產量的主要因子是貯藏根萌發之前和膨大期間乾物量不足，樹冠光合成與植物受到之日射有密切關聯(Agata and Takeda 1982b)，而膨大期間所受之高總日射量已知與高產量有關 (Agata and Takeda 1982a)。而且，膨大時期所累積之50%以上的同化物被輸送到發展中的根(Bhagsari and Harmon 1982)。因此，在貯藏根膨大時期，高日射量和加速現有同化物轉運到發展中的貯藏根對高貯藏根產量是絕對必要的。所以，供源葉供應的同化物可限制積儲產量(Gifford *et al.* 1984)；葉供應愈多同化物給發展中的根，則根數愈多，平均根重愈高。

產量因子之間的負相關經常可見於穀類和蔬菜類(Evans 1975)。這種產量因子之間的負相關經常被解釋爲產量受同化物的供應量所限制。然而，甘藷中並無此種產量因子之間的負相關 (Bouwkamp and Hassam 1988)。

如果光合成限制貯藏根產量，我們可預期較高產量的繁殖系表現出較高的光合成率。這個條件之重要性在於光合成率可能與產量平行；但是，如以上所討論，它們之間存有任何正相關的證據並不多，也沒有任何實例可證明選擇較大光合成率導致產量的增加。因此，就甘藷而言，同化養分的生成量並非產量的主要限制因子，養分的運送與分配（積貯强度）等遺傳特性才是關鍵。在整個生長期增加二氧化碳的濃度也許可增加總乾物量和生物量分配到貯

藏根。Bhattacharya *et al.* (1985)發現貯藏根膨大對二氧化碳增加的正面反應；膨大的貯藏根在增加二氧化碳的情況下比例上比芽輸送更多的同化物。結果顯示供源潛力可藉二氧化碳的增加而造成貯藏根產量的大幅增加，也就是說，供源潛力可能受限，但增强的供源潛力也可調節積儲强度而促進貯藏根的膨大。

(四)供源－積儲結論

上述證據表示基因型將同化物分配到貯藏根的能力對於決定生產潛力很重要，而貯藏根對同化物的需求對於供源潛力可產生顯著的激發效應。這暗示積儲强度比潛在供源對貯藏根產量更具決定性。調節積儲强度輸入同化物至貯藏根的確實機制尙不確定。供源潛力和積儲强度也許好像平衡雖然積儲强度可能事實上受限制。同化物增加而貯藏積儲不增加不會提高產量，而貯藏積儲增加同化物不增加也可導致貯藏根不易膨大。因此，供源潛力和積儲强度都可視爲限制貯藏根形成。唯有使供源與積儲間同化養分貨暢其流，才能達到兩者間經濟栽培上的平衡點。

四、供源潛力和積儲强度的改善

雖然甘藷繁殖系之供源潛力和積儲强度有顯著差異，直到最近其相對關係的重要性才被應用在甘藷繁殖系的改進上 (Li and Kao 1985a)。Hahn 和Hozyo (1984)建議培育兼具高供源和高積儲的雜交品種以進一步增加產量。然而，高供源品系和高積儲品系之間的雜交品種是否會產生高供源高積儲的後代則有待查證。

總乾物量顯然有品系間的差異 (Pardales and Belmonte 1989; Tsuno 1971; Tsuno and Fujise 1963)。改進高供源可望獲得到高乾物量及高貯藏根產量，雖然品系之間存有光合成效率和淨同化物率的差異(Hahn and Hozyo 1984; Sadik 1973)，但比較供源參數和總乾物量之間並沒有一致的相關。因此，篩選供源潛力似乎不合效益。嫁接法取而代之被用來篩選供源 (Hahn 1982)； 然而，未曾有過高供源潛力與高乾物量間關聯性之報告。因此僅以增加供源潛力，來提高貯藏根產量的機會不大。僅管如此，在最後生長階段評估總乾物量可能值得嘗試。由於最後乾物量是供源的整合，它可能是整個生育時期的供源潛力與有效分配的較好指標。

從上述證據看來，積儲潛力影響貯藏根產量甚於供源潛力。因此只選擇高積儲强度可能較容易改善甘藷的產量。高積儲强度會導致某種程度的供源和輸送效率的改進。產量和積儲强度容易平行增加直到達到供源潛力所設的限制。一旦達到此階段，積儲强度及供源潛力都必須或多或少同時加强，才能有進一步的發展。在這情況下，兼顧兩種特性方能有效改良品系。積儲强度遠比供源潛力容易確認、評估、及選擇。嫁接法時常應用在篩選生產潛力(Yoshida *et al.* 1987)和相對積儲强度 (Hahn 1977; Hahn and Hozyo 1984; Li and Kao 1985b)上。然而，貯藏根數和平均貯藏根重是植物育種學家最常用來測量積儲强度的參數。發展中貯藏根的維管束數量也被認爲是區別繁殖系在貯藏根累積乾物能力的指標(Lu *et al.* 1981 and 1983)。當遺傳上產量之決定因素已經明確，而我們也能自品系間偵測到這些基

因，則可藉基因工程進一步改進產量。

貯藏根的數目、大小、和潛在生長率無疑是積儲强度的重要決定因素，但是後者是否決定於輸送效率，酵素轉換，或貯藏過程，有沒有受到積儲產生的生長調節激素的影響，尙不清楚。評估輸送效率的一個方法是使用收穫指數 (Li 1986; Tsuno and Fujise 1964a)。葉比重可能也可做爲評估積儲强度的另一參數。

要充分的評估田間生長植物的任何一個係數所需樣本一般說來數量大而費力，這是供源潛力和積儲强度的評估工作不易進行的原因之一。不過，葉插法(Spence 1971) 因爲所費材料和時間較少，已被應用在這一方面之研究(AVRDC 1988; Kato *et al.* 1972; Nakatani *et al.* 1988a and 1988b)。葉插法利用單一供源植物系統和田間生長植物之間的關係，可提供供源潛力、葉比重、總乾物量(圖4)、積儲强度、貯藏根產量(圖5)、收穫指數 (圖6)、和澱粉累積過程等係數的種間差異之訊息 (AVRDC 1990a and b)。葉插的轉換接木被用來探討同化物的輸送 (Spence and Humphries 1972)，以及評估產量潛力和供源潛力與積儲强度的相對重要性(Nakatani *et al.* 1988a)。

總之，改良甘藷的最佳方法似乎是提高總乾物量和收穫指數。評估總乾物量和收穫指數也比評估與這些參數有關的個別生理性狀容易。選擇高積儲强度將大幅度的改善收穫指數。葉插法可快速而有效地評估總乾物重和收穫指數。

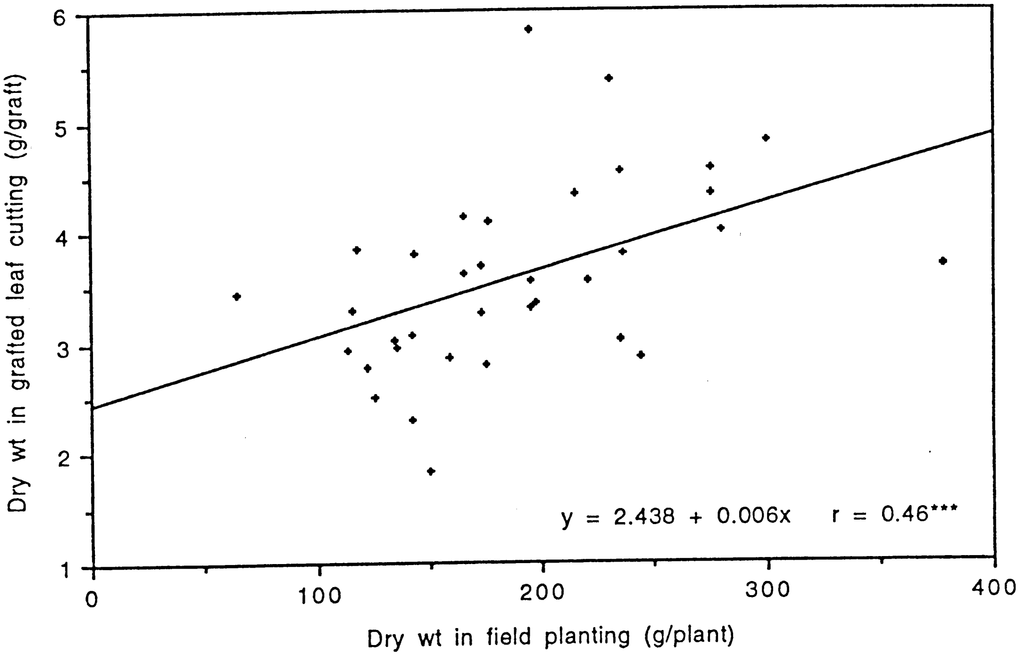

Figure 4. Relationship of total dry matter production between the field trial and the self-grafted leaf-cutting test of 35 sweet potato clones.

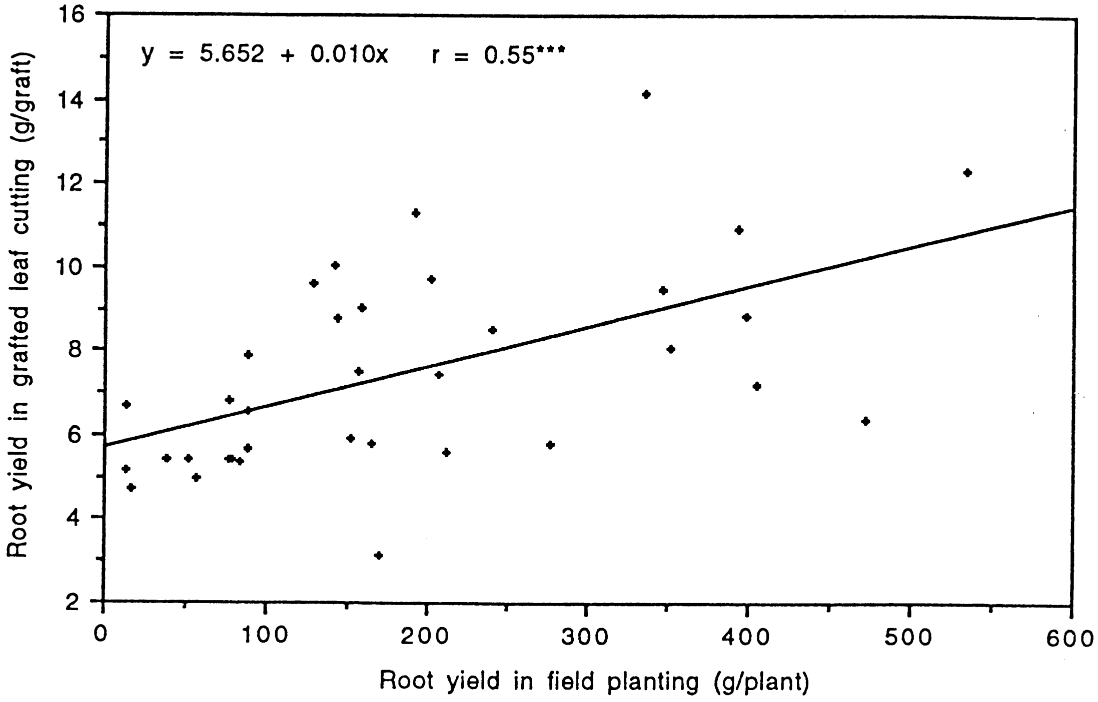

Figure 5. Relationship of storage root dry weight between the field trial and the self-grafted leaf-cutting test of 35 sweet potato clones.

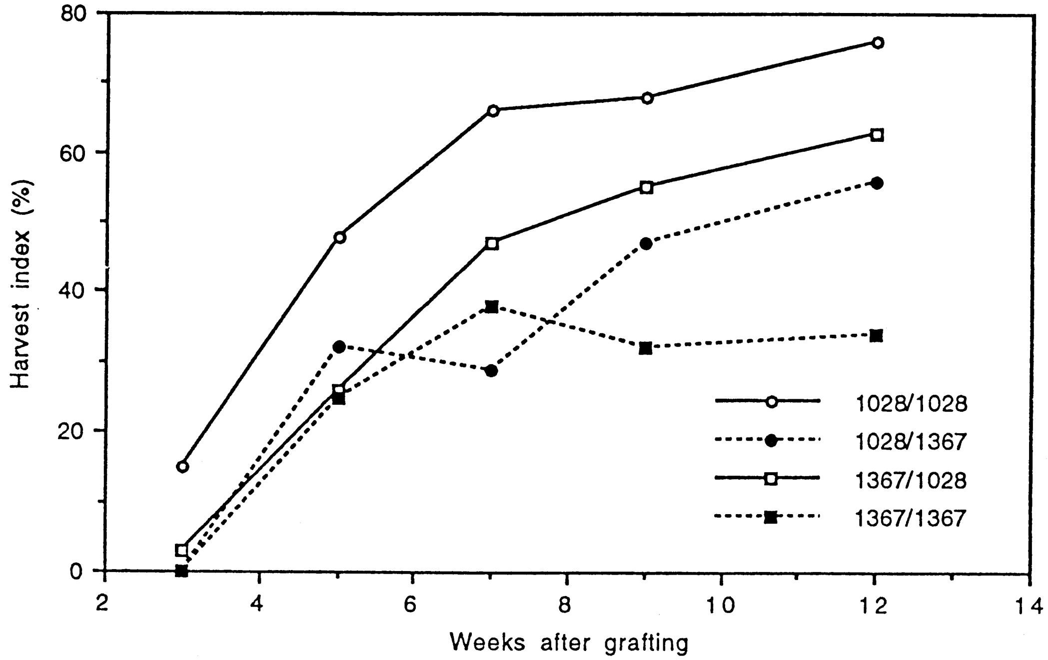

Figure 6. Changes in harvest index of of self and reciprocally grafted (scion/stock) leaf cuttings of two sweet potato clones, CN 1028-15 and CN 1367-2,during the growth period of 2 to 14 weeks of growth.

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The Source-Sink Relationship and Yield Performance of Sweet Potato

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ABSTRACT

The nature of the source-sink relationship has been widely investigated in sweet potato with the intent that acquired information would lead to an understanding of yield-forming processes and to overcome limiting factors. There are marked differences in sink strength and source potential of sweet potato clones. Both source potential and sink strength are important in determining the yield of sweet potato. However, the evidence indicates that sink strength more than source potential affect photosynthesis and translocation, and that the sink strength thereby regulates dry matter production and yield formation in storage roots. Furthermore, since the source in sweet potato is a more complex component than the sink, it seems probable that for yield improvement, either through genetic means or management practices, can be achieved more easily by improving the sink strength. Once the sink strength reaches its limit set by source potential, further progress requires both increased source potential and sink strength in a more or less coordinated manner.

(Key Words : Sweet potato, sink, source, dry matter production, dry matter partition, yield.)